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Visuohaptic convergence in a corticocerebellar network

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Abstract

The processing of visual and haptic inputs, occurring either separately or jointly, is crucial for everyday-life object recognition, and has been a focus of recent neuroimaging research. Previously, visuohaptic convergence has been mostly investigated with matching-task paradigms. However, much less is known about visuohaptic convergence in the absence of additional task demands. We conducted two functional magnetic resonance imaging experiments in which subjects actively touched and/or viewed unfamiliar object stimuli without any additional task demands. In addition, we performed two control experiments with audiovisual and audiohaptic stimulation to examine the specificity of the observed visuohaptic convergence effects. We found robust visuohaptic convergence in bilateral lateral occipital cortex and anterior cerebellum. In contrast, neither the anterior cerebellum nor the lateral occipital cortex showed any involvement in audiovisual or audiohaptic convergence, indicating that multisensory convergence in these regions is specifically geared to visual and haptic inputs. These data suggest that in humans the lateral occipital cortex and the anterior cerebellum play an important role in visuohaptic processing even in the absence of additional task demands.

Introduction

Visuohaptic (VH) object perception is highly relevant in our everyday life and its noninvasive investigation recently became a focus of multisensory research. Several studies investigating haptic processing in visual cortex have consistently shown that neural processing of objects in the two modalities converges in the so-called lateral occipital complex (LOC; Amedi *et al.*, 2001; Malach *et al.*, 1995; see also Amedi *et al.*, 2005 and Lacey *et al.*, 2009 for reviews).

Other studies on haptic sensory acquisition (Gao *et al.*, 1996; reviewed in Barlow, 2002) and illusory visuotactile processing (see Makin *et al.*, 2008 for a recent review) also suggest VH convergence for specific regions of the human cerebellum. Moreover, an increasing number of studies have investigated the neural basis of VH convergence by searching for activation increases during visual and haptic stimulation. VH convergence effects were found in several cortical regions, including the bilateral insula (Hadjikhani & Roland, 1998; Banati *et al.*, 2000; Holdstock *et al.*, 2009) and perirhinal cortex (Holdstock *et al.*, 2009), as well as anterior (Grefkes *et al.*, 2002) and posterior (Saito *et al.*, 2003) intraparietal sulcus (IPS).

These previous VH convergence studies have used matching tasks requiring the participants to match the inputs across sensory modalities, and to indicate their decision with a motor response (Hadjikhani & Roland, 1998; Banati *et al.*, 2000; Grefkes *et al.*, 2002; Saito *et al.*, 2003; Nakashita *et al.*, 2008; Holdstock *et al.*, 2009). Matching demands are known to involve memory (e.g., O'Neil *et al.*, 2009) and attention (e.g., Thompson & Duncan, 2009) processes which may be hard to disentangle from activations reflecting multisensory convergence on the perceptual level (see also Holdstock *et al.*, 2009). Moreover, in some of the studies visual and tactile stimuli were presented sequentially (Hadjikhani & Roland, 1998; Grefkes *et al.*, 2002), whereas others used simultaneous bimodal stimulation (Banati *et al.*, 2002; Holdstock *et al.*, 2009; Nakashita *et al.*, 2008; Saito *et al.*, 2003). The convergence of sequentially and simultaneously presented bimodal inputs might impose different demands on neural integration mechanisms which, in addition to differences in task difficulty, might account for the apparent inconsistencies of the reported findings.

In a recent study, Tal & Amedi (2009) presented congruent or incongruent visual and haptic stimuli, without explicit task demands. However, the bimodal inputs were presented sequentially, which did not allow for investigating the convergence of simultaneous

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visual and haptic inputs. Instead, the authors contrasted congruent and incongruent VH sequences to examine crossmodal repetition suppression effects, which were found in the lateral occipital tactile–visual region (LOtv), a subregion of the LOC, the calcarine, parietal and prefrontal sulci, and the insula (Tal & Amedi, 2009).

Our study aimed to investigate the convergence of simultaneous visual and haptic shape information without additional task effects. Based on the results of the studies described above, we predicted that VH convergence effects would occur in a distributed network of brain regions, including LOC, IPS, insula and anterior cerebellum, if activations in these regions reflect VH convergence independently of top-down task demands.

We conducted a VH main experiment using unfamiliar artificial 3-D objects (Fig. 1A). These stimuli were presented either visually, haptically or bimodally. The only instruction was to remain attentive throughout the experiment. Passive stimulation was used to minimize the effects of additional cognitive demands. Three additional experiments were conducted in order to control for the motor aspects of haptic perception and to test whether VH convergence regions might also be involved in audiovisual (AV) or audiohaptic (AH) convergence.

Materials and methods

Participants

Sixteen healthy adults (eight females, mean age 29.1 years, range 22–38 years, one left-handed) participated in Experiment 1. Of these 16 participants, 13 also took part in Experiments 2 and 3, and 14 in Experiment 4. All participants had normal or corrected-to-normal vision and hearing. They received information about the functional magnetic resonance imaging (fMRI) procedure, and a questionnaire to check for potential health risks and contraindications. Volunteers gave their written informed consent after having been introduced to the procedure. The study was approved by xxx and was in accordance with the Declaration of Helsinki.

Stimuli and procedure

In the two VH Experiments 1 and 2, participants were presented with images of four unfamiliar artificial 3-D objects (Fig. 1A) and/or actively touched these objects (wooden fribbles; http://www.cnbc.cmu.edu/tarrlab/stimuli/novel-objects/fribbles.zip/view.html; Fig. 1A). In the AV control Experiment 3, we employed gray-scale images and vocalizations of eight familiar animals. The AH control Experiment 4 involved four 3-D toy versions of familiar animals (Fig. 1B) and their corresponding vocalizations. Each experiment consisted of both unimodal and bimodal experimental conditions during which stimuli were presented simultaneously.

Within block designs, experimental conditions were presented for ~20 s (16 s in Experiment 3) corresponding to ten (Experiment 3, eight) measurement volumes separated from the next block by a fixation baseline period of equal length. Each single object stimulus was presented for 2 s. In the studies including haptic processing (Experiments 1, 2 and 4), closure and re-opening of the participants' grasping right hands were cued by color changes of a centrally presented fixation cross. Subjects did not see their hands during haptic stimulation. In Experiments 2 and 4 we additionally controlled for these color cues and the motor components of the grasping task. This was accomplished by an additional control condition during which participants merely closed and re-opened their right hand, without any additional sensory stimulation. In Experiment 3, participants were only instructed to fixate and remain attentive during the measurements. Each experiment consisted of four (Experiment 3, five) experimental runs each including all experimental conditions twice in randomized order.

The stimuli were presented with Neurobehavioral Systems (Albany, CA, USA) Presentation software running on a PC (Miditower Celeron) at a frame rate of 60 Hz. Images were projected onto a vertical screen positioned inside the scanner with an LCD projector (VPL PX 20; Sony) equipped with a custom-made lens. Participants viewed the screen through a mirror. Mirror and projection screen were fixed on the head coil. The participants' field of view was 52.5° visual angle (maximum horizontal distance). Visual stimulation consisted of gray-scale photographs (mean stimulus size, 19.7° visual angle) which were presented in the center of a black screen. Auditory stimuli were presented through an fMRI audio system (Commander XG; Resonance Technology, Northridge, CA, USA; frequency response, 100 Hz to ± 25 kHz). Participants perceived sounds simultaneously at both ears via headphones.

Imaging

fMRI was performed with a 3-Tesla Magnetom Allegra scanner (Siemens, Erlangen, Germany) at the Brain Imaging Center, Frankfurt am Main, Gremany. A gradient-recalled echo-planar imaging sequence was used with the following parameters: 34 slices; repetition time, 2000 ms; echo time, 30 ms; field of view, 192 mm; in-plane resolution, 3×3 mm^2; slice thickness, 3 mm; gap thickness, 0.3 mm. For each subject, a magnetization-prepared rapid-acquisition gradient-echo sequence was used (repetition time, 2300 ms; echo time, 3.49 ms; flip angle, 12°; matrix, 256×256; voxel size, $1.0 \times 1.0 \times 1.0$ mm^3) for detailed anatomical imaging.

Data analysis

Neural correlates of object-related multisensory convergence were assessed in each of our four experiments using the so-called max-criterion [i.e. VH > max (V,H) in Experiments 1 and 2, AV > max(-A,V) in Experiment 3 and AH > max(A,H) in Experiment 4], where V is visual, H is haptic and A is auditory. We thus searched for regions that were (i) significantly activated during each of the respective unimodal conditions and (ii) responded more strongly to bimodal stimulation than to either of the respective unimodal conditions. These criteria are held to be sufficiently strict and appropriate for the definition of multisensory convergence effects in human neuroimaging studies (Beauchamp, 2005; Doehrmann & Naumer, 2008; Goebel & van Atteveldt, 2009).

Data were analyzed using the BrainVoyager™ QX software package (version 1.9; Brain Innovation, Maastricht, The Netherlands; Goebel *et al.*, 2006). Preprocessing of functional data (including spatial smoothing with a Gaussian kernel of 8 mm), volume-based statistical analysis using a random-effects general linear model (Experiment 1, df = 15; Experiment 2, df = 12), and correction for multiple comparisons were performed as described in greater detail in recent work from our group (Hein *et al.*, 2007). Statistical maps were initially thresholded at $t = 3$; $P < 0.009$, uncorrected. A cluster-size thresholding technique (Forman *et al.*, 1995) was then used to correct for multiple statistical comparisons. Applying a minimum cluster size of 268 mm^3 resulted in a corrected threshold at $P < 0.05$. The data from Experiments 2, 3 and 4 were also analyzed based on regions of interest (ROIs) in the same bilateral LOC and anterior cerebellar

COLOR

FIG. 1. Experimental stimuli of the VH Experiments 1 and 2. Subjects viewed images of unfamiliar objects (wooden fribbles; A) and/or actively touched them. All objects were presented in both unimodal (V and H) as well as bimodal (VH) conditions. VH combinations consisted of touchable 3-D objects (right panels) presented to the subject's right hand and the presentation of corresponding gray-scale photographs (left panels), which were presented simultaneously at the center of the subject's visual field. Each single stimulus was presented for 2 s and closure and re-opening of the right hand was cued by a color change of a centrally presented fixation cross.

regions which were identified as sites of VH convergence in Experiment 1.

Results

The first analysis aimed to identify brain regions of VH convergence. To do so, we conducted a $0 < V < VH > H > 0$ statistical conjunction. Applying this max-criterion, we found convergence-related clusters ($t_{15} = 3$, $P < 0.05$, corr.) in bilateral anterior lobe regions (lobules V and VI; Schmahmann *et al.*, 1999, 2000) of the cerebellum and the bilateral LOC (upper and lower halves of Fig. 2, respectively). Further details regarding the exact location and the extent of spatial activation of each of these ROIs is provided in Table 1. In addition, the anterior cerebellar location of the above reported VH convergence effects was confirmed at the single-subject level (see Supporting Information for details).

Given that the cerebellum traditionally is considered to be involved in motor learning and control (e.g. Glickstein, 1992, 1993), it is possible that the observed anterior cerebellar effects reflected motor processing rather than VH convergence. To test this alternative explanation we conducted a second VH experiment with the same basic design and an additional cue- and motor-control condition in which subjects merely closed and re-opened their right hand, without receiving additional sensory stimulation (see also Materials and methods). In this second experiment, we again found VH convergence effects in bilateral anterior lobe regions (lobules V and VI) of the cerebellum ($t_{12} = 3$, $P < 0.05$, corr.; blue-colored clusters in the upper panel of Fig. 3), overlapping with the anterior cerebellar convergence regions revealed in Experiment 1 (orange-colored clusters in the upper panel of Fig. 3; see also Fig. 2).

In addition, we compared the results of the cue- and motor-control condition with the effects of unimodal (i.e. V and H) stimulation in these anterior cerebellar ROIs as identified in Experiments 1 (Fig. 3; middle row) and 2 (Fig. 3; lower row). The unisensory V and H conditions showed stronger activations than this control condition.

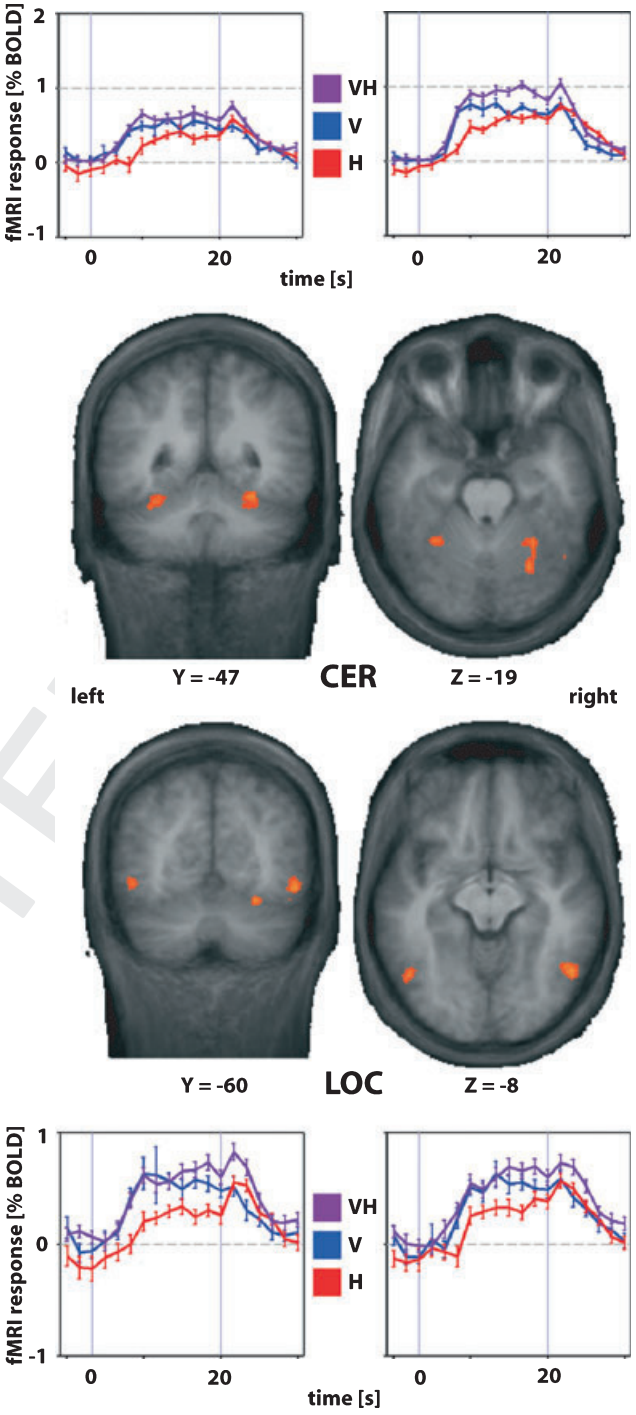

FIG. 2. Bilateral VH convergence in LOC and the anterior cerebellum. Brain regions involved in VH convergence of unfamiliar 3-D stimuli (i.e. fribbles) in Experiment 1 were determined employing the max-criterion (i.e., $0 < V < VH > H > 0$). Statistical maps were based on a random-effects general linear model ($t_{15} = 3$; $P < 0.05$, corr.) and corrected for multiple comparisons using a cluster-threshold estimation algorithm (Forman *et al.*, 1995). VH convergence was found in a bilateral corticocerebellar network including lobule V (and VI) regions in the anterior cerebellum (CER; upper panels) and the LOC (lower panels). The panels in the central rows show coronal (left column) and transversal (right column) slices of a group-averaged anatomical dataset and provide the respective *Y*- and *Z*-coordinates in Talairach space. The plots show mean activation time courses (± SEM) for the respective regions in the left and right hemispheres. Color coding is provided in the center of each row. Table 1 provides further details regarding the exact location and spatial activation extend of each ROI.

TABLE 1. Regions of VH convergence

ROI	Talairach co-ordinates (mm) *x*	*y*	*z*	Number of voxels
LOC				
Left	−46	−60	−7	292
Right	47	−57	−8	753
Anterior cerebellum (lobules V and VI)				
Left	−29	−46	−19	333
Right	26	−51	−18	1002

Regions were determined by a random-effects general linear model (based on Experiment 1). Max-criterion contrasts ($0 < V < VH > H > 0$) for the investigation of VH convergence were calculated on a whole-brain level. The resulting statistical map was initially thresholded at $t_{15} = 3$; $P < 0.009$. A cluster-size thresholding technique (Forman *et al.*, 1995) was then used to correct for multiple statistical comparisons. Applying a minimum cluster size of 268 mm^3 resulted in a corrected threshold at $P < 0.05$. Talairach coordinates are derived from the clusters shown in Fig. 2 and are provided in millimeters. The number of voxels is based on the resolution of the anatomical data set, i.e. $1 \times 1 \times 1$ mm^3.

Taken together, the results of Experiments 1 and 2 provide robust and retest-reliable evidence for VH convergence in bilateral anterior lobe regions (lobules V and VI) of the human cerebellum. In the next step, we tested whether these cerebellar regions play a more general role in object-related multisensory processing or whether they are specifically involved in the convergence of V and H inputs.

To investigate this question, we conducted two control experiments with a similar experimental design to the VH experiments but different modality combinations. In Experiment 3, we presented object sounds and object images in isolation or simultaneously. In Experiment 4, we used auditory and haptic stimuli, or combinations of the two. Whole-brain analyses revealed no hint for AV ($t_{12} = 3$, $P < 0.05$, corr.) or AH ($t_{13} = 3$, $P < 0.05$, corr.) convergence effects in the cerebellum. In addition, we investigated AV and AH convergence effects in our bilateral anterior cerebellar and LOC ROIs (as identified as regions of VH convergence in Experiment 1). This analysis did not provide any evidence for AV (Fig. 4, middle panel) or AH (Fig. 4, right panel) convergence, either in the anterior cerebellar or in LOC ROIs. This indicated that multisensory convergence in these regions was specific to V and H inputs.

Discussion

The aim of this study was to investigate VH convergence while minimizing top-down task effects. Our results show that this rather bottom-up driven VH convergence is related to increased activation in a bilateral corticocerebellar network. The anterior cerebellar regions which were revealed have previously been shown to be involved in both haptic and visual processing (e.g. Gao *et al.*, 1996; Hadjikhani & Roland, 1998; Saito *et al.*, 2003; see Barlow, 2002 and Makin *et al.*, 2008 for reviews), but were not reported as main findings in studies focusing on VH convergence (as reviewed in Amedi *et al.*, 2005 and Lacey *et al.*, 2009).

In contrast to our study, previous VH convergence studies have used matching tasks, in which participants were required to match inputs from the same or different modalities. In the case of different modalities, this might have imposed additional processing load regarding memory processes or attention which might have influenced the mechanisms of VH convergence (Holdstock *et al.*, 2009; see also van Atteveldt *et al.*, 2007; Baier *et al.*, in press). Our study suggests

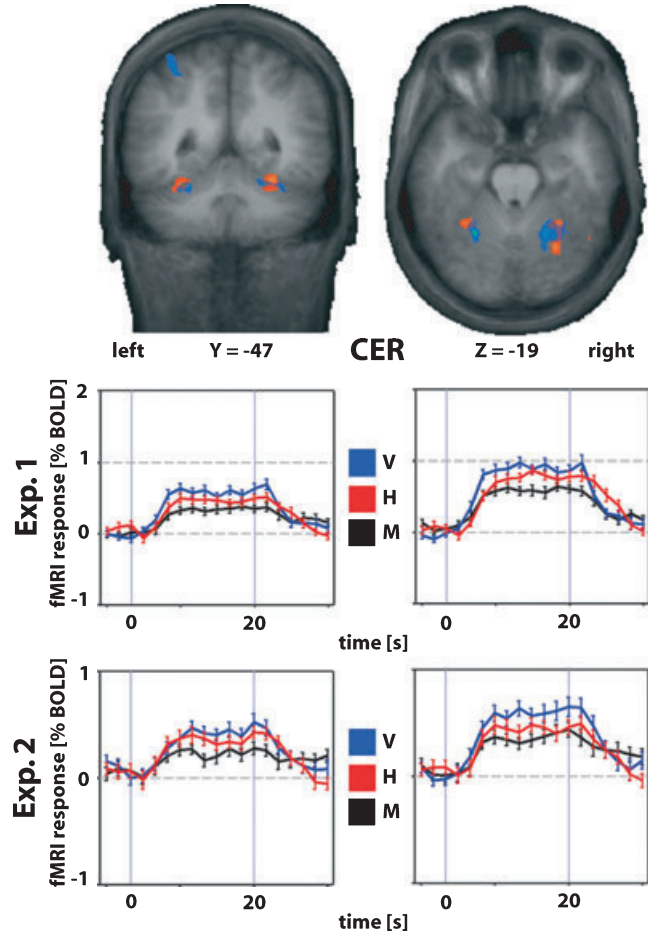

FIG. 3. Retest reliability of VH convergence in the anterior cerebellum. In Experiment 2, VH convergence effects [VH > max(V,H)] in lobule V (and VI) of the anterior cerebellum (upper panel, blue-colored clusters) overlapped with corresponding activation clusters from Experiment 1 (orange-colored clusters), thus replicating the main finding of Experiment 1. In addition, unisensory (i.e., V and H) activations (± SEM) in these ROIs (from Experiment 1, middle panels and Experiment 2, lower panels) were found to exceed those during our cue- and motor-control condition (M), indicating true sensory processing in these ROIs during H as well as V stimulation.

that in the absence of such task effects VH convergence can be found not only in the LOC but also in bilateral regions of the anterior cerebellum.

The crucial role of the LOC in human object processing is well established. Originally, it was described as a visual ventral stream region preferentially activated by images of intact (as compared to scrambled) objects (Malach *et al.*, 1995). It is important to keep in mind that the LOC is a very extended occipitotemporal region which consists of two main parts, namely a more anterior–ventral part in posterior fusiform gyrus and a more posterior–dorsal lateral occipital (LO) part (Grill-Spector *et al.*, 2001). To date, robust tactile or haptic activations in response to shape stimuli have mainly been reported for the LO part of the LOC, which has consequently also been termed LOtv (Amedi *et al.*, 2002). In addition to our findings, it has been repeatedly shown by others (see Lacey *et al.*, 2009; for a recent review) that this LOtv part is not usually activated by auditory object stimuli in conventional fMRI experiments. However, sensitivity of the LOC to auditory object information has been shown when using sophisticated AV fMRI adaptation designs (Doehrmann *et al.*, in press) or other imaging techniques such as event-related potential source localization (Molholm *et al.*, 2004). It has also been demon-

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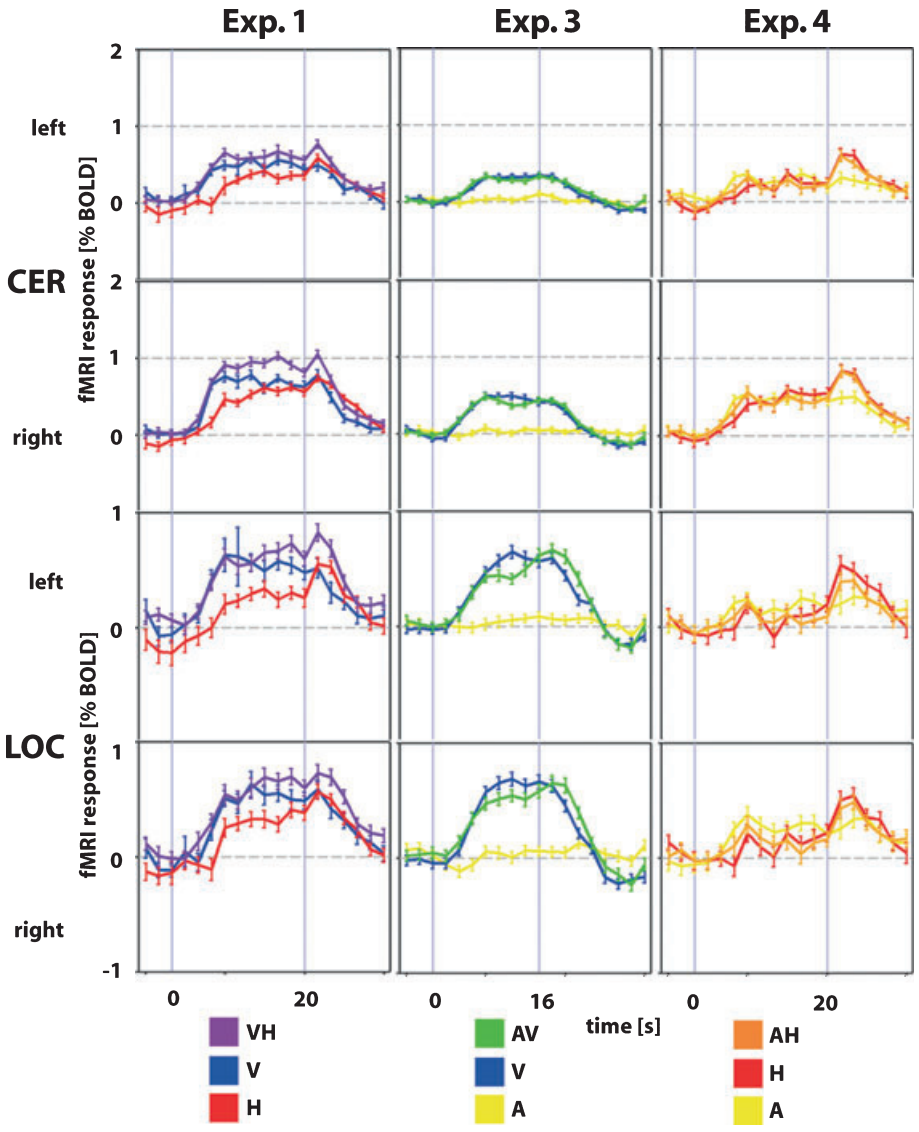

FIG. 4. ROI-based analysis of bisensory selectivity. In order to test whether the VH convergence regions from Experiment 1 (as shown in Fig. 2) selectively integrated information from the V and H modalities, we conducted AV and AH control Experiments (3 and 4). Employing the max-criterion [i.e. AV > max(A,V) and AH > max(A,H), respectively], we found hints for neither AV (middle panels) nor for AH (right panels) convergence in any of the anterior cerebellar (CER; two upper rows) and LOC (two lower rows) ROIs. For each of these ROIs, the figure provides the activation profiles (± SEM) during the AV and AH experiments (3 and 4) in comparison to the VH experiment (1; left panels).

strated that LOC activation correlates with the auditory representation of 3-D shape in subjects using a visual-to-auditory sensory substitution device (Amedi *et al.*, 2007). Taken together, there is growing consensus that this region is a "metamodal operator" (see Amedi *et al.*, 2005 and Lacey *et al.*, 2009 for reviews) which processes shape information irrespective of the particular input modality. Confirming this assumption, our data show that LOC is activated by both visually and haptically presented unfamiliar objects, and the processing of visual and haptic object features converges in this region independently of additional task demands. Auditory object features, however, carry comparatively little shape information and thus do not activate the LOC (or the anterior cerebellum), at least not in standard fMRI experiments (Amedi *et al.*, 2002). Confirming this assumption, our results did not reveal any auditory or AH LOC (or anterior cerebellar) activations in Experiment 4 when comparing these activations to the cue- and motor-control condition.

In contrast to LOC, very little is known about the role of the anterior cerebellum in multisensory processing. Previous fMRI studies in humans (Gao *et al.*, 1996; see Barlow, 2002 and Makin *et al.*, 2008 for reviews) have suggested that the human cerebellum is crucially involved in the processing of both haptic and visual inputs. In line with these findings, single-cell data from nonhuman primates have shown that the mammalian cerebellum receives multisensory inputs from prefrontal regions and from sensorimotor (Kelly & Strick, 2003; Ramnani, 2006) and visual (Glickstein *et al.*, 1994; Kralj-Hans *et al.*, 2007; Sultan & Glickstein, 2007) association cortices. The vast majority of such cerebellar inputs via the pons stem from cerebral sensorimotor and visual regions, in particular from the dorsal visual stream (as reviewed in Sultan & Glickstein, 2007). These strong connections to both sensorimotor and visual cortices make the cerebellum an ideal candidate for VH convergence.

However, our study is among the first to show VH convergence in anterior cerebellar lobules V and VI (Schmahmann *et al.*, 1999, 2000). Supporting our findings, a recent study found VH interaction effects in the anterior cerebellum (Stevenson *et al.*, 2009). As the focus of this study was on inverse effectiveness, subjects were stimulated with visual and haptic stimuli with varying salience. Stevenson *et al.* (2009) identified VH interaction effects based on the criterion of superadditivity (VH > V + H) instead of the max-criterion used in both the present and previous studies (see Beauchamp, 2005; Doehrmann & Naumer, 2008; Goebel & van Atteveldt, 2009 for an overview). The converging evidence from Stevenson *et al.* (2009) and our results underlines the validity of both analysis strategies (max-criterion and superadditivity) to identify sites of multisensory convergence, and further stresses the validity of the reported VH convergence in the anterior cerebellum.

The revealed anterior cerebellar regions are an integral part of the human sensory–motor network (Toro *et al.*, 2008). It is usually activated in concert with a number of prominent cortical regions (SI, SII, LOtv, etc.) as well as subcortical structures (thalamus and basal ganglia). Anterior cerebellar activations are frequently found with a marked ipsilateral bias (with regard to the actively touching hand). This reflects the rather ipsilateral gross connectivity pattern of the cerebellum in general and clearly contrasts to the well-known contralateral activation bias usually seen in most cortical sensory–motor regions. More than a decade ago it was convincingly shown (Gao *et al.*, 1996) that these anterior cerebellar regions play an important role in the active acquisition of tactile information. In particular, it is assumed that they serve fine-grained sensory–motor optimization processes in order to achieve an optimal positioning of the respective tactile receptor surfaces of the actively touching hand. During the bimodal VH conditions of the experiments reported here the visual modality provided 3-D structure information earlier than the haptic modality. In this context, the visual components of our bimodal stimuli might have immediately triggered sensory expectations regarding input in the haptic modality. Based on recent effective connectivity evidence from our lab (van den Bosch *et al.*, 2009), we assume that the reported anterior cerebellar regions facilitate multisensory convergence not only through the above-mentioned optimization of active tactile information acquisition but also by feeding back the respective information to the LOtv part of the LOC. Based on this interpretation, we predict that marked anterior cerebellar activations such as those reported here should be more easily detectable in studies investigating active touch than in investigations involving only passive tactile stimulation.

These findings support the notion that cerebellar functions contribute to a variety of domains and are not limited to motor learning and control, as traditionally assumed (Glickstein, 1992, 1993; Strick *et al.*, 2009). The VH convergence regions observed in the anterior cerebellum proved to be retest-reliable, and their activation profiles indicated robust sensory processing during unimodal (i.e., V and H) stimulations. Moreover, VH convergence effects in both anterior cerebellar and LOC regions were also found to be significant in contrast to our cue- and motor-control condition, and thus are unlikely to reflect cue- or motor-related processing.

We also tested whether the human anterior cerebellum plays a general role in multisensory convergence, or whether it is specifically involved in the convergence of V and H inputs, in two control experiments with AV and AH stimulation. Neither whole-brain nor ROI-based analyses revealed any hints for AV or AH convergence effects in the LOC or anterior cerebellum. This result sheds light on the multisensory specificity of these regions, indicating that they are preferentially involved in the convergence of V and H inputs (Amedi *et al.*, 2002, 2007; Stevenson *et al.*, 2009).

To conclude, our results provide retest-reliable evidence for VH convergence in bilateral LOC and anterior cerebellar regions, which play an important role in human VH convergence, in the absence of additional task demands. This finding contributes to a better understanding of human corticocerebellar circuits as well as the distributed neural mechanisms of multisensory integration.

Supporting Information

Additional supporting information may be found in the online version of this article:

Fig. S1. Anterior cerebellar VH convergence in individual subjects.

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Abbreviations

A, auditory; AH, audiohaptic; AV, audiovisual; fMRI, functional magnetic resonance imaging; H, haptic; IPS, intraparietal sulcus; LOC, lateral occipital complex; LOtv, lateral occipital tactile–visual region; ROI, region of interest; V, visual; VH, visuohaptic.

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